THE BIOLOGY OF SAN JOSE SCALE ON PEACHES WITH SPECIAL REFERENCE TO THE BEHAVIOR OF MALES AND JUVENILES[1]

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INTRODUCTION

SAN JOSE SCALE, *Quadraspidiotus perniciosus* (Comst.), has continuously infested deciduous fruit orchards in California since its introduction into the United States in 1870. Although it can be kept under control with winter sprays, it sometimes recurs and gains much headway before its presence is noticed.

The research herein reported was designed to supply needed data on the biology and bionomics of San Jose scale in the peach belt of California's interior valley. The trends of its behavior on peaches are discussed for out-of-doors and greenhouse situations. Included also are observations on the significance of males, the moulting process, and the formation of the shell-like covering.

GEOGRAPHICAL DISTRIBUTION

San Jose scale is destructive in most of the principal deciduous fruit-growing regions of the world. It is especially serious in temperate and subtropical regions. It is reported from the Orient, Australia, New Zealand, Russia, Germany, Austria, Africa, the Mediterranean region, Canada, and South America. England and the Scandinavian countries are believed to be free of the pest. It is prevalent in California, perhaps because so many of the preferred hosts are grown here commercially.

HOSTS

Fairly detailed lists of susceptible hosts have been published in various countries. It must be noted, however, that although such host lists are the result of experiment or observation, they should be considered in relation to the place of observation. The degree of susceptibility can vary within varieties and for given varieties in different climates.

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Among some 700 hosts listed so far, the most susceptible fruit trees and vines are found in the genera *Prunus, Pyrus, Cydonia* and *Ribes.* Among ornamentals, the genera *Crataegus, Populus, Ligustrum, Salix, Sorbus, Rosa,* and *Syringa* are very liable to attack.

INJURY TO HOSTS

San Jose scale infests all of the surface parts of young host plants, from ground level to the tips of the shoots. On mature trees, infestations occur mostly on branches with bark tissues showing light to moderate suberization. Ascending crawlers disperse from these areas to invade new suitable wood. Leaves and fruits are also colonized when infestations are severe. The scurfy incrustations are easily overlooked because the covers of the insects superficially resemble the normal lenticels of bark.

A characteristic halo-like, red discoloration appears within 24 hours after new crawlers settle on tender peach wood or on potato tubers which they are sometimes forced to select. The discolored areas increase in diameter as the age of the nymphs advances. In densely infested spots, the rings of color coalesce with those produced by other, nearby nymphs. The red cortical tissue swells with accumulating sap. The bark often cracks and exudes gum. Areas immediately surrounding the punctures made by the insects subsequently become dark brown and gelatinous. A gradual desiccation of the cortical tissues follows. Heavily infested peach twigs have been observed to die back within four months after arrival of the first crawlers.

If sample areas of the outer bark are trimmed from mature or semimature infested branches, the damage will often show in the cortex as necrotic patches surrounded by reddish sap-laden tissue. The scale population tends to invade new, undamaged areas whereas the old affected branches are likely to become infested with boring insects. An undetected infestation is able to kill young trees within three years. Unchecked, vigorously reproducing infestations on mature trees permanently affect their structure, vigor, and productivity.

Recent histological research by Enser (1941), in Austria, reveals the destructive effect produced by the mouth parts of the insect on the cambium of host trees. Sections of wood cut through the points of attachment of the insects show that the rostralis penetrates the cortex into the deeper-lying cambium. Growth of the pierced cambium is suspended or impaired. If impaired, the associated xylem and phloem cells differ in number, size, and arrangement from those found in normally formed tissues. The aberrant cortical growth produces a crater-like lesion.

The physiology of damage to host tissues by San Jose scale is not well understood. Chemical and other functional relationships between the insects and host tissues, the nature and effect of the insect's saliva on plant cells, et cetera, are fertile areas for investigation.

METHODS OF DISPERSAL

San Jose scale is generally believed to be passively carried great distances in shipments of nursery stock, scions, and budwood.

The natural spreading of the pest by its own powers of locomotion is

limited to very short distances. This is because the crawlers—the infectious motile stage—are able to creep only very short distances on plant surfaces during their brief free-living existence. Wind, birds, insects, and orchard workers are the chief factors in the passive spreading of crawlers between trees, orchards or neighboring localities.

Ants apparently do not carry or nurture the young of this species (Marek, 1952). The ants are indifferent to the presence of adult scale insects in their pathways since San Jose scale, like other Diaspinae, does not secrete honeydew. However, Marek observed that crawlers sometimes fasten themselves to the legs of ants and ride in that position or elsewhere on their bodies.

Contact between branches of adjacent trees is one avenue of dispersal within mature orchards. Melis (1943), as well as the present writers, have observed that crawlers are unable to creep on either wet or dry soil. Moreover, the writers have brushed numerous crawlers directly onto the surfaces of terra cotta dishes on which rested clean potato tubers. No infested tubers were obtained with this procedure. But crawlers transferred readily from infested to uninfested tubers in terra cotta dishes when there were points of contact between the potatoes. Crawlers liberated by adults on cut peach twigs maintained in nutrient solutions were able to infest potted peach trees when leaves of the latter were placed in contact with the cut twigs.

OVERWINTERING STAGES

According to Marlatt (1906), San Jose scale passes the winter in half-grown stages protected by small, black covers.

In Central Europe, San Jose scale is reported to overwinter exclusively as first nymphs—in the "sooty black-cap" phase—whereas all other stages are eliminated by low winter temperatures. The overwintering period in Central Europe usually lasts from September to May. Klemm (1944) has reported on the extreme cold-hardiness of the sooty black-cap phase in Russia. According to his observations, prolonged exposure of this stage to a temperature of –30° C produced only 80 per cent mortality. Nymphs of this growth stage were able to moult when temperatures were raised to 10° C.

All of the developmental stages overwinter in Southern Europe, but second nymphs preponderate during the months of January and February (Melis, 1943; Pegazzano, 1948; Grandori, 1950). According to Melis, a true hibernation of the insect does not appear to exist in areas characterized by mild winters. The relatively mild winter climate of Southern Europe retards its development but does not stop it.

Periodic samples of infested wood taken from commercial orchards in the Sacramento Valley during one season showed that approximately 80 per cent of the scale population overwintered as inactive first nymphs (fig. 1). The remaining 20 per cent of the wintering forms were mostly gravid adult females, many of which had already delivered most of their crawlers. Included were also a few nongravid adult females and trace numbers of second nymphs. This status persisted with almost no change from November through mid-January. A marked shift in the composition of the populations began in the latter part of January. The first nymphs resumed their growth actively and, within a relatively short period of time, transformed into second
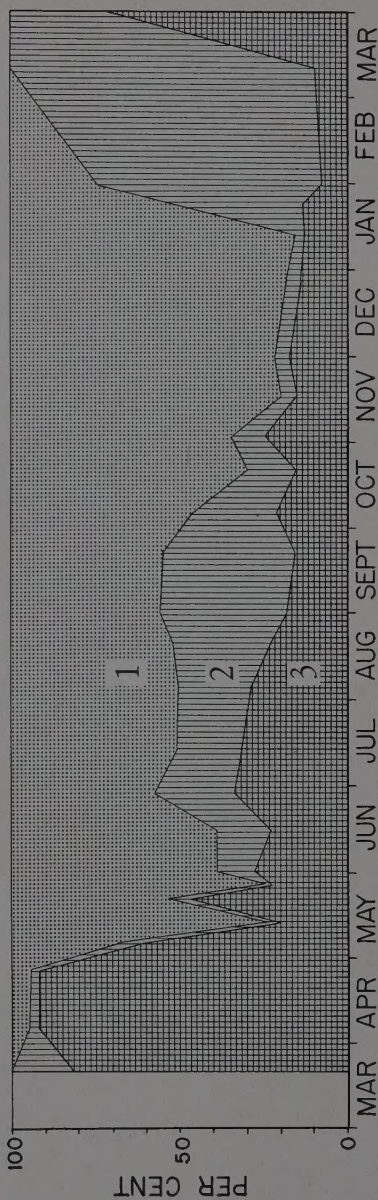
Fig. 1. Diagram to show seasonal changes in composition of populations of San Jose scale on peach bark. Only three nonmotile stages are here represented as the entire population of each sample. Ordinate shows per cent of individuals in these stages as determined for orchard samples of approximately 500 viable individuals of all categories (except crawlers and adult males). Modesto, California, 1953–54.

Legend: 1. Stippled area = first nymphs (white-cap and black-caps, but not crawlers). 2. Vertical lines = second nymphs. 3. Crosshatch = adult females.

nymphs. At the close of February almost no first nymphs could be found. The second nymphs moulted and became adults during March. This second moult produced young, unmated females and males of the prepupal stage. The second moulting period coincided with the blossom and petal-fall periods of the host trees.

More detailed information about the overwintering tendencies of San Jose scale in this locality was obtained through studies of controlled populations and isolated individuals. The term "first nymph" is employed here in an inclusive sense, to designate the instar between hatching (or parturition) and the first moult. The term applies to the crawler, white-cap, and black-cap phases of the instar.

TABLE 1

DEVELOPMENT DURING WINTER OF COLONIES OF CRAWLERS ISOLATED ON PEACH WOOD IN SEPTEMBER. DATA BASED ON 340 INDIVIDUALS SECURED AT END OF OBSERVATION PERIOD. DAVIS, CALIFORNIA, 1955–56

Stages classified	Per cent representation of stages in subsamples averaged for time intervals given below							
	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar. 1–19	Mar. 20–31
First nymphs—black-caps	100	45	18	63	81	56	7	..
First nymphs—dead	..	..	..	..	..	6	..	..
Second nymphs—males	..	24	..	..	..	4	22	..
Second nymphs—females	..	29	..	..	..	4	22	..
Second nymphs—dead	..	..	27	..	..	..	16	..
Prepupa + pupa—males	..	..	..	..	..	..	..	8
Adult females—nongravid	..	..	24	..	..	..	..	22
Adult females—gravid	..	..	..	37	19	30	29	16
Adult males—under scale covers	..	2	31	..	..	..	..	24
Adults—dead	..	..	..	..	..	..	4	30

The winter history of a colony of crawlers established during September on a limb of a scale-free peach tree is shown in table 1. The growth stages of the population were determined by means of samples taken on small chips of bark removed at intervals of 7 to 10 days. The changes are shown as variations in percentages of each of the different stages in relation to the totals observed in each of the samples. The number of undisturbed individuals allowed to continue their development until the final sampling date is given as "Adults secured."

This procedure showed that some of the juveniles developed to adulthood before December. These then wintered as mature females, most of which contained embryonated eggs. But others persisted unchanged as first nymphs in the black-cap phase until late January. Those which resumed growth at this time attained adulthood in late March or early April. It therefore appears that the spring brood of new adults originated principally from over-wintered first nymphs.

Some of the first nymphs appearing in summer generations were also observed to persist overlong in this stage of development. These juveniles did not moult until the end of summer. This diapause-like condition per-

sisted for 40 to 45 days. A comparable phenomenon has been described for San Jose scale in Russia and Switzerland. According to Timofeieva (1937) and Geier (1950), this species is fundamentally bivoltine and is character- ized by a nymphal diapause. They have noted that many first nymphs of each generation undergo diapause whereas others of the same generations continue to develop without interruption. The factors governing temporary cessation of development are not known.

Crawlers isolated at Davis during November showed a pronounced tend- ency to become quiescent. An entire sample population of crawlers settled on two-year peach wood in November remained as first nymphs until February (table 2). Other masses of crawlers settled on potato tubers during November

TABLE 2

DEVELOPMENT DURING WINTER OF COLONIES OF CRAWLERS
ISOLATED ON PEACH WOOD IN NOVEMBER. DATA BASED
ON 171 INDIVIDUALS SECURED AT END OF OBSERVATION
PERIOD. DAVIS, CALIFORNIA, 1955–56

Stages classified	Per cent representation of stages in subsamples averaged for time intervals given below					
	Nov.	Dec.	Jan.	Feb.	Mar. 1–19	Mar. 20–31
First nymphs—black-caps	100	100	100	74	27	..
First nymphs—dead	..	..	..	7	8	..
Second nymphs—males + females	..	..	..	19	65	..
Second nymphs—dead	..	..	..	..	..	55
Prepupa + pupa—males	..	..	..	..	..	19
Adult females—nongravid	..	..	..	..	..	26

and left to overwinter in a lath house were similarly affected. This period of dormancy on the part of the scale population coincides with the period of winter dormancy of the peach host. It is also the period of lowest winter tem- peratures in this mild climate (table 3).

The fact that few, if any, second nymphs develop during midwinter is probably related to moderately low average temperatures and, possibly, host inactivity. There is, however, another factor accounting for the scarcity of second nymphs during winter. Few individuals of this stage are able to sur- vive the winter period. In order to substantiate this point, a batch of crawlers was transferred on November 9 (1955) to two potted peach trees which had been kept for a time in the greenhouse. On December 12, the majority of these individuals was found to have completed the first moult and was be- ginning to show sex differences in the structure of their covers. On this latter date, one of the infested trees was moved from the greenhouse to an out-of- doors lath house. At the end of January new adults were on the tree left in the greenhouse. Some of these were releasing crawlers. Meanwhile the second nymphs on the tree in the lath house did not develop. The final status of this population was determined on February 16, 1956. The scale covers were lifted and the insects were examined microscopically. Most of the population was found to have perished in the second nymphal stage; there were a few living first nymphs which, presumably, were tardy in their development prior

to transfer out-of-doors. The viable ones were just beginning to moult, according to the pattern described for orchard populations.

There is also a notably high mortality among moulting first nymphs (table 2: second nymphs—dead). Dead individuals of this class appear to be teneral second nymphs encased in the hardened first-nymphal exuviae. This occurs even in populations reared indoors.

Unfertilized females artificially isolated from males in the fall did not survive later than the end of January. Although the alimentary canal did not atrophy immediately in these females, their bodies remained small and ulti-

TABLE 3

AVERAGES OF OUTDOOR MONTHLY TEMPERATURES AND RELATIVE
HUMIDITIES RECORDED WHILE OBSERVATIONS WERE
IN PROGRESS. DAVIS, CALIFORNIA, 1955–56

1955	Temperature (degrees Fahrenheit)			Relative humidity (per cent)		
	Maximum	Minimum	Mean	Maximum	Minimum	Mean
January	49.8	35.3	42.6	94.4	67.3	80.8
February	59.8	37.0	48.4	83.2	39.1	51.6
March	67.1	41.0	54.0	94.7	31.4	63.0
April	66.7	41.3	54.0	84.0	34.9	59.4
May	80.7	51.2	65.9	82.0	29.0	55.5
June	86.9	53.1	70.0	82.0	26.1	54.0
July	91.5	53.6	72.6	83.5	23.2	53.3
August	95.5	53.0	74.2	85.2	18.4	51.8
September	91.0	53.4	72.2	82.0	21.6	51.8
October	80.8	47.8	64.3	87.5	30.9	59.2
November	63.8	41.5	52.7	86.2	47.2	66.7
December	55.7	43.9	49.8	97.1	70.1	83.6
1956						
January	50.1	42.3	46.2	98.0	77.2	87.6
February	57.5	36.4	47.0	88.5	44.4	66.4
March	67.4	40.6	54.0	86.0	36.3	61.1

mately became flat and transparent. They were reduced to dry, lifeless pellicles during February. Other unfertilized females responded similarly when isolated during summer or winter. It is thus possible that the unfertilized females perished after depleting food reserves accumulated during development and which would otherwise have been utilized in ovigenesis.

Physical factors of the environment clearly affect those stages of the insect which have no intimate connection with subsurface tissues of the host— crawlers and final instars of the male line. Prolonged exposure to temperatures below 50° F and heavy precipitation appear to be lethal for the above-mentioned stages as well as for settled crawlers not advanced beyond the white-cap phase of follicle formation. No free crawlers were found on orchard trees during December, 1955. There were, however, many dead crawlers imprisoned beneath the follicles of their mothers. Orchard infestations observed during the period of January through March, 1956, comprised chiefly first nymphs and adult females filled with embryonated eggs. Only insignificant numbers of crawlers, parturient females, and males older than first nymphs were found on the samples of bark examined during this period.

LIFE CYCLES DURING SPRING AND SUMMER

It was possible to follow only the grosser trends of seasonal population change in commercial orchards. Small chips of bark were cut from infested trees and all of the insects on a number of these were examined and classified in order to determine relative numbers of the several developmental stages. One series of samplings was started in March, 1953, and continued thereafter for one year. The changes in the composition of these infestations are illustrated for three of the nonmotile stages in figure 1.

It is apparent that first nymphs represented the dominant stage in orchard populations from May to January. The proportion of first nymphs was greatest during November, December, and part of January. Second nymphs outnumbered all other stages only during February. The numbers of individuals in this stage were minimal during the fall and again in April and May. Adult females constituted the bulk of the population during March and April. Information secured in this manner agrees reasonably well with observations made during 1955–56 on mass cultures of isolated crawlers.

The development of males was more completely examined in another series of samples of orchard populations made during 1955–56. This series showed clearer cyclical trends in the emergence peaks of males. Although males emerged steadily in modest numbers throughout the growing season, four noticeable peaks were recorded: 1) March–April, 2) June, 3) August, and 4) October–November. Generally, however, the lapping of generations during summer made it too difficult to follow the rise and fall of discrete generations in samples of this sort.

Additional data on life history were derived principally from restricted populations cultured on potted peach trees kept out-of-doors. Batches of crawlers were transferred from pieces of infested bark to the trunks and two-year-old branches of uninfested host trees. The transferral was accomplished by tying bundles of infested pieces of bark to selected parts of the new hosts for periods not exceeding 24 hours. Desired parts of the new trees were thus populated with crawlers released within this brief period. In order to localize each new population so established, the selected parts of the trees were blocked off with bands of "Deadline." A succession of new populations was established in this manner during the growing season. The insects were examined at frequent intervals by cutting away samples of bark for microscopic examination. Cyclical events and duration of stages were therefore determined by sacrificing a part of every population on each sampling date. This study was started when crawlers of the first generations began to appear in good numbers during May, 1955, and was terminated when overwintering populations matured during March, 1956.

Individuals belonging to the first generation are known to have been present from April to October, 1955. Those of the first generation which were isolated during early May completed development and bore young during July and August. Those isolated later in May produced young during August and early September. Although none were isolated during June, it is probable that they would have matured still later in September and October. Adult males required 36 to 49 days to develop from crawlers isolated in May (table

4). Since there was a peak emergence of males in orchard trees during June, the males undoubtedly originated from crawlers of the first generation released during April or May.

The earliest date on which crawlers of the second generation appeared could not be established precisely. But it is known that crawlers isolated in May matured and bore young 68 to 77 days later (table 4). Their first appearance was therefore not appreciably earlier than the beginning of July. Crawlers isolated during July produced young during September and October; those transferred in early August produced young from October well

TABLE 4

AVERAGE NUMBER OF DAYS REQUIRED FOR DIFFERENT STAGES
IN THE LIFE CYCLE OF SAN JOSE SCALE ON OUTDOOR
PEACH TREES. DAVIS, CALIFORNIA, 1955

Dates on which crawlers settled	Duration of stages: average number of days					Number of males "secured"	Number of females "secured"
	Combined nymphal stages	Females			Males		
		Prepar- turitional period	Parturi- tional period	Total life span	Combined nymphal stages		
May 9................	43	34	40	117	45	31	12
May 16................	36	32	...	...	36	10	14
May 27................	45	27	44	116	49	15	13
July 11................	49	30	58	137	59	4	15
July 18................	42	29	50	121	48	5	10
August 8................	41	44	51	135	42	7	18
August 25.............	43	..	..	...	43	10	5
September 16..........	50*–195†	..	..	...	54*–196†	36*–44†	100*–11†
November 4...........	146	..	..	...	149‡	..	22

* Population completed development in late autumn; adult females overwintered with embryonated eggs.
† Population overwintered in the black-cap stage and completed development in the following spring.
‡ To pupal stage.

into December. Orchard samples showed a peak flight of males in late August. The time required for the development of males reared from crawlers isolated in July was 48 to 59 days, which would fix their time of birth as late June or early July.

Crawlers isolated from orchard populations during September—from females of both first and second generations—showed the characteristic behavior already described in the foregoing account of overwintering tendencies. Some of these matured during November and overwintered as gravid females. A much larger number of them persisted through the winter months as first nymphs. Masses of crawlers isolated during November wintered *in toto* as first nymphs.

According to the information obtained from orchard samples and from mass cultures of crawlers on potted trees, San Jose scale produces at least three generations per year in this locality. The approximate duration of each generation is illustrated in figure 2. Adult females of the first generation which mature during July and August produce few crawlers late enough to winter as first nymphs. Adults of the second generation which mature in

September and October give rise to both maturing and wintering young of a third generation. The flight of males observed in October and November comes mostly from the maturing fraction of third-generation nymphs. The spring flight of males observed in March and April comes from the over-wintering fraction of third-generation nymphs. In other words, some of the third-generation males mature during late fall whereas others do not mature until early spring.

Although females of the third generation overwinter in both adult and first-nymph stages, both categories of individuals begin to reproduce almost in synchrony in the spring.
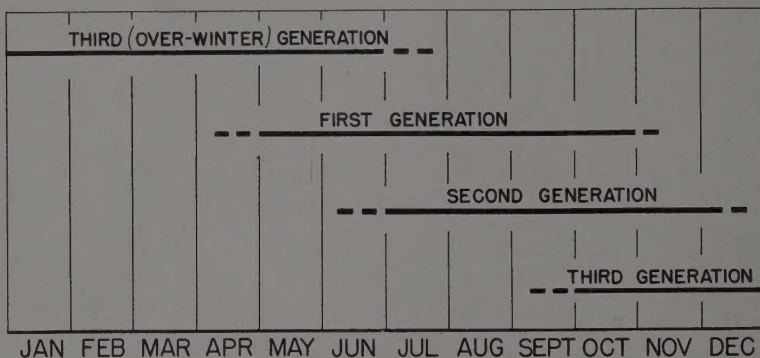

Fig. 2. Schematic representation of periods during which three generations of San Jose scale occur on peach trees. Broken lines used to show that beginning or ending of each cycle was not determined precisely.

The conclusion that this species undergoes two almost complete genera-tions and a partial third is confirmed by observations made on variations in numbers of reproducing females encountered in successive orchard sam-plings. Graphic presentation of these data (fig. 3) shows three noticeable maxima of reproductive activity during the growing season of 1953. The first coincided with the build-up of first-generation crawlers released by females of the overwintered generation. The second peak, in August, occurred when adults of the first generation were releasing crawlers of the second generation. And the final peak, in October–November, marks the period during which second-generation adults were most actively producing crawlers of a third generation. The numbers of reproducing individuals were proportionately fewest during March or April—each end of the graph—just when the winter populations of juveniles transformed into new adults.

CRAWLERS REARED ON POTATO TUBERS

Others have discovered that some species of scale insects can be reared on potato tubers (Clausen, 1956). This technique was used successfully in this study for supplemental observations on the behavior of juveniles. Populations

cultured on potatoes in the laboratory and greenhouse provided a much more convenient situation to regulate and examine than that offered by peach trees. Batches of crawlers were allowed to transfer to the tubers for 24-hour periods. The infested tubers were then placed on terra cotta plates and covered with glass cylinders closed at the tops with muslin. Individuals as well as aggregates of individuals were isolated on parts of the tubers with rings of "Deadline." Developmental trends in the aggregates were determined by sacrificing some of the individuals at each examination. It was possible to rear some of these insects continuously on the same tubers for as long as eight months—for four full generations.
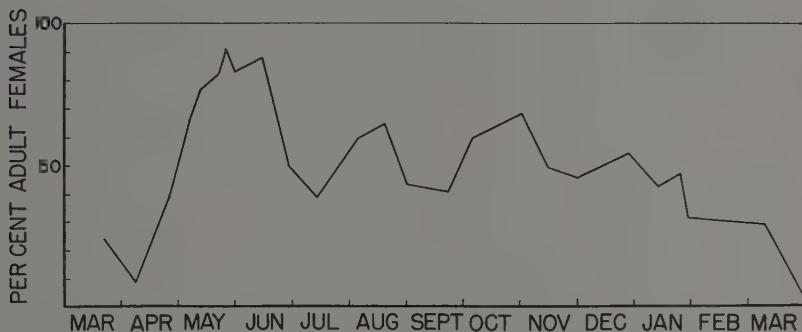

Fig. 3. Seasonal fluctuations in numbers of reproducing females (gravid and parturating) encountered in successive samplings of an orchard infestation. The ordinate axis represents the per cent of reproducing individuals in populations of adult females. Modesto, California, 1953–54.

IMPORTANCE OF MALES

Data obtained in this study indicate that San Jose scale does not reproduce parthenogenetically (table 5). Females isolated in their nymphal stages from contact with males completed development on natural or substitute hosts, and died two to five months later without issue and without showing any indication of having produced embryonated eggs.

Selected nymphs were isolated on orchard peach trees by picking away all others and covering them with small, modified Munger cells. Individuals and aggregates on potted trees and tubers were isolated in the greenhouse by continuously eliminating all developing males at the second nymphal stage and by caging the females under cotton-stoppered glass vessels or in sleeve cages. The usual muslin of sleeve cages was replaced with paper in order to prevent the ingress of the tiny winged males.

Approximately one month after the final moult, virgin females tended to exsert their pygidia from beneath their scale covers. The pygidia were observed to move slowly but almost ceaselessly in a short arc. After six weeks or longer in the adult stage, the bodies of the virgins began to show antemortem symptoms: reduction in size, transparency, and desiccation.

BIRTH AND REACTIONS OF JUVENILES

The females of this species are ovoviviparous. Embryonated eggs may develop within the bodies of females in 10 to 15 days after fecundation. The birth of the first crawlers usually occurs between 30 to 40 days after copulation and continues thereafter for six to eight weeks under orchard conditions.

The size of the broods produced by individuals has been reported by a number of observers. According to Marlatt (1906), the average number of crawlers issuing from females on fruit trees in the United States is about 400.

TABLE 5

OBSERVATIONS ON THE DEVELOPMENT OF ISOLATED, UNFERTILIZED
FEMALES. DAVIS, CALIFORNIA, 1955

Dates on which crawlers settled	Total number of times cultures inspected	Average number of days		Final number of females "secured"
		Combined nymphal stages	Adult life without progeny	
Individuals reared on potato tubers in greenhouse				
August 28...	25	28	161	15
September 13..	20	38	61	10
Individuals reared on peach trees in greenhouse				
November 4..	13	31	58	6
December 12...	12	26	54	20
Individuals observed on peach trees outdoors				
September 16..	21	49	105	10

They are released at the rate of 9 to 10 every day for almost six weeks. Lüdicke (1950) found that San Jose scale in Germany produces from 50 to 200 crawlers per individual. Gerassimova (1937) recorded three to four generations for the species in the south subtropical zone of the U.S.S.R. (Souchi), and a maximum of 145 crawlers for females of the second generation. In the temperate zone of East Georgia and the northern Caucasus, this observer found that the number of offspring per female ranges from 100 to 135 and that there are only two and one-half broods per year. Timofeieva (1937) noted maxima of 87 crawlers per female of the first generation and 137 for females of the second generation in East Georgia. Another Russian observer, Popova (1938), counted 100 to 110 crawlers per female, but there was no particular tendency for the numbers to vary according to generation. Females reared on potato tubers in the greenhouse at Davis, California, averaged only 37 to 62 crawlers. The smaller number in this case may relate to the change of host.

Many of the anatomical details of the embryos can be recognized before birth. Especially striking are the spiral filaments of the rostralis, one coil on

each side in the middle third of the embryo. Prepartim females weave an opening for the exit of crawlers through the pygidial area of the scale covers. An arched exit is fashioned with bands of secretion which line and support the uplifted margin of the scale cover. The female also liberates a special birth secretion around the pygidium in the form of a soft, whitish cushion. These observations on the weaving of the arched exit agree in general with an earlier description given by Disselkamp (1954).

The duration of the birth process and the shedding of the chorion by young of this species have been described by Marlatt (1906), Lüdicke (1950), and Melis (1951). Lüdicke's observations were more complete because he developed a method of replacing the naturally formed scale covers with artificial caps fashioned of cellophane. His findings were confirmed in the present work by the use of parturient females affixed to potato tubers. A segment of the scale cover overlying the brood chamber was cut away from a number of females to allow for observations with minimal disturbance to the parent.

Birth is accomplished within a matter of one or two minutes. The newborn crawler is egg shaped and covered with a delicate, unbroken chorion which momentarily adheres to the vaginal orifice. Several newborn crawlers often stick together with a viscous fluid, presumably of vaginal origin. This adhesion phenomenon is more often observed toward the end of parturition, when clusters of dead crawlers may be found glued together in the brood chamber of almost every old reproducing female.

The breaking of the chorion and the first movements of appendages begin within 30 minutes after birth. When the brood chambers are exposed by lifting the scale covers it is sometimes possible to see new crawlers wobbling about with the chorion still adhering to their caudal bristles. Dried remnants of the chorion persist in the brood chamber as small flakes, frequently glued together in clusters. Crawlers leave the brood chamber either in supine or prone positions, mostly during the warmer periods of morning. Low temperatures and rain appear to prevent their escape.

The peak of emergence occurs near the middle of the parturitional period and declines toward the end. Females sometimes die before all of the eggs are expelled; and, near the end of parturition, incompletely developed embryos may be extruded. The total life span of females, as given in table 4, does not include any period survived after parturition ends. The duration of postpartim life, if any, was not determined.

FREE-LIVING PERIOD

Crawlers observed in exposed brood chambers start to migrate soon after birth. The interval between birth and the beginning of migration varies from 2 minutes to 24 hours. Those of the second category often die without settling.

Most of the crawlers affix themselves to the host within one to four hours after leaving the brood chamber. Once emerged, they first creep slowly then more rapidly. Progression follows a zig-zag pattern and the linear distance traversed is limited. The greatest distance covered in one direction is reported by Skorkin (1937) to be approximately 3 meters. An average rate of travel is less than a meter per hour (Lüdicke, 1950). In the final analysis, however, the distance of travel and the duration of the free-living phase are

conditioned by surface texture of the host plant, extent of damage to host by prior generations, humidity, temperature, vitality of the crawler, et cetera.

The crawlers tend to settle in clusters, mostly near their mothers. Late in autumn, they frequently settle in crevices close to buds of the plant. They also tend to move in an ascending direction on vertical surfaces. Intense sunlight is avoided. Masses of crawlers released onto unshaded twigs from chips of infested bark settled almost entirely on host tissue underlying the chips. In one instance it was noted that all of the individuals affixed under the protective cover of donor chips failed to survive as white-caps when the chips were removed to admit sunlight. Many crawlers settle beneath empty scale covers, some within the brood chambers of the mother insects.

AFFIXATION AND MOULTING

The first waxy secretion is produced on the dorsum of migrating crawlers. When, somehow, a suitable location is found, the rostralis is forced into the substrate. Once settled, the erstwhile crawler assumes a lenticular shape and folds its legs and antennae beneath its body. A loose meshwork of wax fibers forms a protective cover, the "white-cap," within 24 hours. Within four to seven days the white-cap evolves into a dense felt-like cover having a characteristic fluffy apical tuft. A band of dark secretion appears around the periphery of the white-cap after the fifth to ninth day. This marks the beginning of the black-cap phase. The covers of nymphs destined to become females begin to undercut the surface tissues of the host at this time. The expanding margins of the growing cover push into the substrate so that the surface layers of the latter come to overlap the rim of the shell. Adult females reared on potatoes are frequently covered almost to the central nipple by a suberized layer of host tissue.

The nymph is capable of limited pivotal rotation about the anchored rostral stylets. The rotary movement and the flexures of the abdomen bring the glandular fields of the pygidium into contact with the periphery of the scale cover. Secreted material is deposited around its circumference. According to Lüdicke (1950), anal excretions are utilized for cementing together the filaments of wax. Incorporation of excrement and fungi (Disselkamp, 1954) may account for the darkening of the scale cover. When this darkens, the individual and its cover are referred to as a "black-cap."

The first moult occurs 18 to 22 days after birth. The moult and subsequent reorganization continue for three to four days. When the cast skin (exuvia) lifts, it completely encases the body of the new second nymph and its dorsal surface is adherent to the interior surface of the scale cover. Internal coils of the new rostralis are visible within the body of the second nymph, as in the case of the first nymph prior to affixation. There appears to be, therefore, a transitional period during which the old mouth parts embedded in the host tissues are discarded and a new attachment is made. The exuvia ruptures at the margins, from head to pygidium. The dorsal portion of the exuvia is incorporated into the scale covering. The ventral part which carries the paired appendages is pressed onto the surface of the host beneath the new nymph. Sex differences are evident at this stage.

A new gray band of material is added to the margin of the scale covering

during the second instar. This material, like the covering of the black-cap, is fashioned from fine filaments of secretion and anal excreta. The apical tuft erodes, leaving behind a central whitish cone, the nipple.

The second or final moult of the female line occurs 20 to 27 days after the first. The second exuvia is also incorporated into the scale covering. The new adult thus formed is larger than the second nymph and is more emphatically pear shaped. The body of the male elongates after the first moult. It acquires a dorsal pair and a ventral pair of eyes. Rotary motions of the body cease but the lamellar growth of the follicle continues in the posterior direction. Ultimate size of the insect and its cover are attained during this instar.

Two characteristic longitudinal grooves develop on the internal face of the scale covering, one on each side, which allow for the expulsion of exuviae formed in later moults and for the liberation of the imago (Marlatt, 1906; Disselkamp, 1954).

Males moult a second time in 10 to 12 days. The individual of the third instar is a prepupa. The second exuvia is not retained but is expelled at the pygidial end of the covering. The proboscis and pygidium are lost during the second moult. Loss of the pygidium indicates that the scale cover is not further enlarged. The digestive tract begins to degenerate. Wing buds and finger-like rudiments of appendages are acquired. Two small bristles and a median 'histoblast' which gives rise to the anal stylus are clearly visible at the caudal end of the prepupa.

A third moult occurs within 6 to 10 days. The exuvia here discarded is a wrinkled, tape-like pellicle. It is expelled. Appendages show well-defined articulations and the stylus evaginates. This instar is the pupa.

The final, fourth moult occurs when the pupa is four to five days old. The exuvia is likewise expelled. The adult backs out of the scale cover with its wings folded forward when the escape is made. Dead males imprisoned under their covers are frequently encountered in population samplings. Whether or not the winged adults can reside beneath their covers for appreciable periods of time after metamorphosis is not known. The imago is orange yellow and possess three pairs of ocellanae, two antennae, a pair of wings with weak venation, and six legs. The intromittent organ, or penis, lies within a ventral groove of the long caudal stylus. Apterous males of this species have been reported only by Melis (1943).

MATING

Males appear to be very weak, intermittent fliers. Those jarred from host material at eye level fly to the ground in a descending spiral course. Air currents generated by greenhouse fans cause them to cling tightly to the host. They move about freely if the fans are stopped. Walking appears to be the chief method of locomotion.

The liberated male immediately cleans its appendages before beginning to wander about. When a female is encountered, the male climbs onto her covering and, with acute flexures of its abdomen, inserts the stylus under her pygidial region. His hind legs are used to assist with the insertion. The motions of copulation continue for only a moment or two. The male then retires

to wander and copulate with other females. One male was observed to mate with three females. And as many as three males have been observed trying to copulate simultaneously with a single female. Whether or not the females are successfully impregnated in each mating operation was not determined.

SUMMARY

Data on life cycle and duration of stages of San Jose scale were obtained from isolated colonies or individuals established on potted peach trees and from samples of infested bark taken from commercial orchards at frequent intervals throughout several seasons. Colonies and individuals reared on a substitute host, potato tubers, contributed supplemental information otherwise difficult to obtain.

Observations based on isolation cultures indicate that this species has three major generations per season, all of which overlap in the fall. Crawlers of the first generation are produced during April, May, and June. Maximum numbers occur during the latter part of May and the first part of June. Those of the first generation mature during July or later and bear young through September. Crawlers of the second generation appear in July and August. This generation matures and bears young during September and October. A third generation of crawlers is produced during September, October, and November. The mixed broods which build up in late fall overwinter as first nymphs or as mature, gravid females.

Some of the crawlers released during September and October mature and mate before the onset of winter. Those released during October and November overwinter as inactive first nymphs in the black-cap phase. Those which pause in the black-cap stage comprise approximately 80 per cent of the population during January. The overwintered first nymphs resume development during February but do not bear young until April or later.

Experiments with isolated virgins show that San Jose does not reproduce parthenogenetically. Unimpregnated females survive for relatively long periods but do not produce embryonated eggs.

Descriptions are given for the birth process, affixation of crawlers to host tissues, moulting and scale cover formation. The geographical distribution, host range, methods of dispersal, and host pathology are also discussed.

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